

Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, U.S.A.

EMILY A. HOLT AND BRUCE MCCUNE

Department of Botany and Plant Pathology, Oregon State University, Cordley
2082, Corvallis, OR 97331-2902, U.S.A.

e-mails: emilyholt@lifetime.oregonstate.edu, bruce.mccune@science.oregonstate.edu

PETER NEITLICH

National Park Service, Western Arctic National Parklands, 41A Wandling Road,
Winthrop, WA 98862, U.S.A.

e-mail: peter_neitlich@nps.gov

ABSTRACT. We sought to assess impacts of fire and grazing by reindeer and caribou on lichen communities in northwestern Alaska. Macrolichen abundance was estimated from 45, 0.38-ha plots. Eighteen of those plots, scattered throughout the southern Seward Peninsula, represented two levels of grazing, heavy and light. We found lightly grazed areas had taller lichens and greater total lichen cover than heavily grazed sites. Minor yet statistically significant changes in community structure were also observed between heavily and lightly grazed sites. However, lichen species richness did not differ by grazing status. Overall, average lichen height appears to be the best indication of grazing intensity on the Seward Peninsula. Apart from the 18 grazing plots, 8 additional plots were established in previously burned sites to represent reference conditions with a known time since disturbance date. These plots provided a framework of vegetation recovery from severe, recent disturbance towards pre-disturbance conditions. Patterns in lichen, bryophyte and vascular plant characteristics from these fire plots in combination with our findings from the grazing plots were then used to interpret the disturbance history of new plots. These new plots comprise the remaining 19 plots (of the total 45) that were sampled within the Bering Land Bridge National Preserve (BELA). We believe the location of BELA, regardless of disturbance history, is more favorable to vascular plants and *Sphagnum*, and lichens grow taller in response, compared to areas on the Seward Peninsula further south. In addition, lower cover in the Preserve may be attributed to site or climatic differences rather than grazing.

KEYWORDS. Reindeer, grazing, fire, succession, lichen height, Alaska tundra.



Over the past century, dramatic fluctuations in caribou (*Rangifer tarandus granti*) and reindeer (*Rangifer tarandus tarandus*) populations in

northwestern Alaska have carried correspondingly variable social, economic and biological consequences. The eastern half of the Seward

Peninsula, including lower portions of the Bering Land Bridge National Preserve (BELA), is historical wintering grounds for Alaska's largest caribou herd, the Western Arctic herd (Dau 2000). In the early 1900s, numbers of native caribou across North America declined (Bergerud 1974). The geographic range of remaining animals in the Western Arctic herd contracted and migration routes shifted east and northward, excluding their traditional rangelands on the Seward Peninsula. In response to reduced numbers of caribou, Russian Chukotka reindeer were introduced onto the Seward Peninsula to initiate reindeer husbandry to overcome food shortages and stimulate local economies (Postell 1990). In less than four decades, the reindeer industry boomed and the number of reindeer peaked at over 600,000 animals, most confined to the Seward Peninsula (Postell 1990). These high numbers quickly declined during the 1930s (Dau 2000). Concurrent with decreasing numbers of reindeer, the Western Arctic caribou herd increased more than six-fold in three decades, and recent census estimates roughly 430,000 caribou in northwest Alaska (Dau 2003). Moreover, the winter range of the Western Arctic herd is shifting back onto the Seward Peninsula into reindeer ranges (Finstad et al. 2002). While caribou numbers on the Seward Peninsula continue to increase, only about 10,000 reindeer still remain in the area today (pers. comm., Rose Fosedick, Kawerak Reindeer Herders Association, Aug 2006).

These extreme shifts in caribou and reindeer occupation of the Seward Peninsula sparked concern regarding rangeland health and quantity and quality of forage. It has, however, been suggested that grazing by native herbivores is part of the flora's evolutionary history, thus cannot be considered a disturbance (Milchunas et al. 1998; Suominen & Olofsson 2000). To varying degrees, cervids have always grazed this region. Reindeer, however, are non-migratory and local herders attempted, until recently, to maintain large herds in allotted grazing ranges (Ihl & Klein 2001). Alternatively, the native grazers, caribou, are migratory and thus intense, persistent grazing pressure is uncommon (Jefferies et al. 1994). During the summer, these animals feed on shrubs, forbs, graminoids, fungi and lichens (Ahti & Hepburn 1967; Holleman et al. 1979). Lichens alone

constitute all or a sizable portion of reindeer and caribou winter forage (Heggberget et al. 2002; Scotter 1967; White & Trudell 1980). Periods during which other forage is largely unavailable can encompass up to two-thirds of a year in these Arctic regions.

Extensive research in the past fifty years has demonstrated that grazing, including both consumption and trampling, can negatively alter lichen communities in Arctic and Antarctic environments (e.g., Ahti 1959; Helle & Aspi 1983; Swanson et al. 1985). Aside from overall reductions in biomass (Gilbert 1974) and decreases in relative lichen abundance (Helle & Aspi 1983), hooves fragment and displace lichens (Cooper et al. 2001; Pegau 1969). Lichen rangeland management, aiming to maintain adequate forage and monitor recovery to gauge grazing rotation periods, is at the center of many Arctic grazing studies (e.g., Gilbert 1974; Klein 1987; Kumpula et al. 2000; Pegau 1970; Virtala 1992). Some work has also focused on free-ranging cervid populations (e.g., Ahti 1959; Arseneault et al. 1997; Boudreau & Payette 2004; Moser et al. 1979). Several sought explanations for migration eccentricities (Ahti 1959; Bergerud 1971; Ferguson et al. 2001) or changes in ecosystem productivity (Manseau et al. 1996). Regardless, the findings are consistent: grazing reduces lichen cover and biomass. Fewer studies, however, have investigated grazing impacts on lichen community structure and diversity. The limited research on this topic has described consistent shifts in lichen community composition associated with grazing (Ahti 1959; Klein 1987; Manseau et al. 1996; Pegau 1970; Tommervik et al. 2004). In contrast, documentation of diversity differences between grazed and ungrazed areas is rather sparse and, where available, inconsistent (Gilbert 1974; Helle & Aspi 1983; Olofsson et al. 2001).

Our study represents a unique assessment of how grazing impacts the amount of lichens, measured as cover and height, as well as lichen community structure and diversity on the Seward Peninsula. Although others have investigated components of these lichen responses to grazing individually, to our knowledge, no other study has considered them all simultaneously in one area. Moreover, the most recent grazing assessment on the

Seward Peninsula was conducted over thirty years ago (Pegau 1970).

We also hoped to use these findings to infer grazing histories of new areas of unknown grazing status. Matching vegetation responses on the landscape to a disturbance history, however, is complicated by grazing being a partially recurring disturbance. So we wanted to integrate information on vegetation recovery following datable events (fire). These chronosequences (e.g., recently disturbed to 50 or more years since disturbance) provides context for evaluating potential grazing effects in these new areas of unknown grazing histories.

On the Seward Peninsula, the main disturbances include grazing, cryoturbation, solifluction movement, volcanic or mining activity, and fire. Fire and volcanism are the two types of these perturbations that are not continual, and fires are the only recent disturbances. Tundra fires in Alaska are infrequent and often restricted to the Seward Peninsula and the Noatak River area (Racine 1981). Based on historical burn data from the past 50 years in BELA, we estimated 444 years, the average fire cycle, would be required to burn an area equal to the size of the Preserve.

We had three primary questions in this study:

(1) Using fire as a dateable disturbance, what is a generalized recovery model for the Arctic tundra dominated by dwarf shrubs and graminoids on the Seward Peninsula? A null model predicts that vascular plant and lichen abundance do not shift over time, nor do they interact or alter each other's abundance. An alternative hypothesis suggests both vascular plant and lichen abundances vary with time since disturbance, and that vascular plants suppress and eventually replace lichens (Fig. 1). In addition to changes in total lichen abundance, what patterns do other lichen community characteristics follow after fire? (2) Is grazing associated with differences in lichen communities on the Seward Peninsula, and if so, what are these differences? We also sought geographic differences in lichen communities, irrespective of grazing, that might confound detection of a grazing effect. (3) Combining information on patterns of recovery following fire disturbances and community changes associated

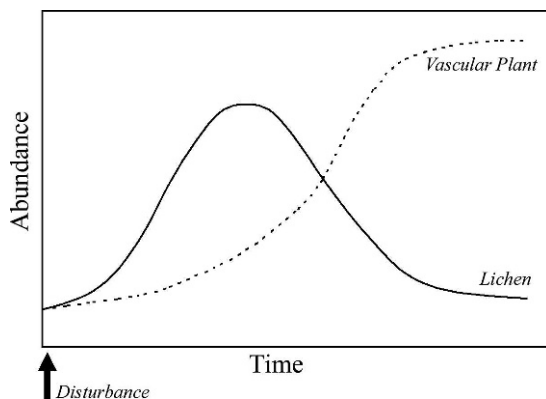


Figure 1. Schematic of our alternate hypothesis of lichen and vascular plant responses to fire. The null hypothesis suggests that abundance of neither responds to the disturbance nor interacts with each other. An alternative hypothesis, shown above, suggests that lichen abundance increases more rapidly than vascular plant abundance, yet declines due to suppression and replacement by vascular plants following disturbance. Dashed line represents vascular plant abundance and solid line represents lichen abundance. Both hypotheses were rejected.

with grazing, what can be inferred about the successional status, or historical grazing impact, of plots from unknown disturbance history within BELA?

MATERIALS AND METHODS

Study area. The Seward Peninsula in northwestern Alaska ($64^{\circ}24'N$ – $66^{\circ}36'N$, $160^{\circ}30'W$ – $168^{\circ}07'W$) has been grazed by reindeer for over one hundred years. BELA, located on the Seward Peninsula, was one of ten protected areas established by the Alaska National Interest Lands Conservation Act of 1980. The act protects both natural and historical resources, while simultaneously maintaining subsistence hunting and reindeer grazing. All 47,200 km² of the preserve are allocated into reindeer grazing allotments managed by the National Park Service and operated by Native permit holders.

Plots were located in the north and central portion of the peninsula (within the preserve boundaries); near the town of Nome at the southwestern tip of the Peninsula; and along the eastern edge of the Seward Peninsula near the town of Koyuk (Fig. 2). Weather stations at the northern and southern tips of the Peninsula are located in

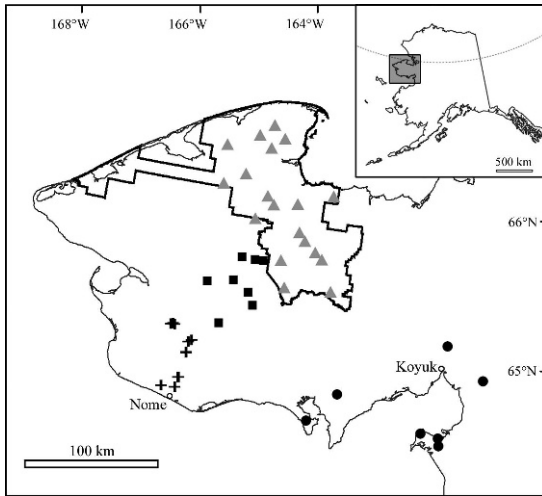


Figure 2. Map of Seward Peninsula, including the Bering Land Bridge National Preserve (heavy black outline). The dashed line in the Alaska inset in the upper right corner represents the Arctic Circle. Gray triangles represent the 19 selected BELA plots, black boxes represent the 8 fire plots and the 18 grazed plots are indicated with black circles and pluses (black circles are the 7 lightly grazed plots in the eastern portion of the Seward Peninsula and pluses represent the 6 heavily grazed and 5 lightly grazed plots on the western Seward Peninsula). Empty circles indicate nearby towns, including Nome and Koyuk.

Kotzebue and Nome, respectively. Consistently gathered weather data were not available for the eastern portions of the peninsula. Mean July temperature in Nome and Kotzebue is 10.6° and 12.4°C, respectively. Mean annual precipitation, falling primarily in late summer, is 44.4 cm in Nome and 28.9 cm in Kotzebue. The common vegetation types present in northwestern Alaska are *Eriophorum* tussock tundra, *Dryas* fell-field, ericaceous-shrub tundra, *Eriophorum-Carex* wet meadow and solifluction slopes (Viereck et al. 1992). Treeline, dominated by *Picea glauca*, encroaches along the southeastern corner of the Seward Peninsula. All our sampling, however, was conducted in tundra sites and did not reflect these boreal communities. Common shrubs are *Salix* spp., *Betula glandulosa* and *Alnus crispa*. The herb layer contains mixed *Eriophorum* spp. and *Carex* spp., *Vaccinium* spp., *Arctostaphylos* spp., *Empetrum nigrum*, *Cassiope tetragona*, *Ledum palustre* var. *decumbens* and *Rubus chamaemorus*. The dominant mosses are *Sphagnum* spp. and *Hylocomium splendens*. The lichen flora is

dominated by species of *Cladina*, *Cladonia*, *Cetraria*, *Peltigera* and *Stereocaulon*.

Sampling. Traditionally, animal exclosures, clipping experiments or repeated observations are used to assess grazing impacts on vegetation. However, exclosures are difficult to maintain in soil underlain by permafrost, and slow lichen growth rates prohibit short-term range assessments. Our grazing classifications, therefore, were based on prior knowledge of reindeer use. We sampled a total of 45 circular fixed-area plots with a 34.7-meter radius. Eighteen of these 45 plots, the grazed plots, occurred throughout the southern portion of the Seward Peninsula, representing two levels of grazing conditions. Two-thirds of these grazed plots (12 plots) were lightly or completely ungrazed, five of which occurred in the Nome area of the western Seward Peninsula in former grazing exclosures and in the Kigluaik Mountains. The remaining seven lightly grazed plots occurred on the eastern Seward Peninsula. These seven lightly grazed plots were originally classified as heavily grazed sites based on historical reindeer grazing accounts (pers. comm., Randy Meyers, BLM-Kotzebue, Jul 2004). Surveys in 2004, however, indicate that these areas do not currently experience heavy grazing, but rather represent lightly grazed sites. The other third of the grazed plots (6 plots), representing our heavily grazed sites, were located immediately adjacent to active reindeer corrals outside of Nome or in areas known to support animals during seasonal handlings. Exact locations of these 18 grazed plots were selected arbitrarily or to maximize proximity to obvious reindeer or caribou activity.

In addition to the 18 grazed plots, we also located 8 fire plots to represent lichen communities that experienced a major, dateable disturbance event in the past 50 years. These eight plots were randomly located within known historic fire perimeters. We acknowledge that fire or landscape conditions may vary, resulting in differential recovery of post-fire vegetation. In more recent burns, burnt tussock bases and blackened soil provided evidence that our plots occurred within burned locations. Otherwise, we had no indication as to the patchiness or intensity of the various fires—merely an outline of their extent. We assumed, therefore, that our plots were large enough

to capture vegetation variability and that our random sampling within a burn allows inference to the entire burn. All the fire plots occurred in a climatically and geologically similar region, and the surrounding unburned vegetation all appeared to be similar dwarf shrub- and graminoid-dominated tundra. The burn dates span between 1954 and 1999, and comprise six different burn years.

Within the preserve, we used a stratified random sample using geographic blocks and GIS land cover data to locate plots (see Holt et al. 2007 for complete description). For the current study, we discarded roughly half the original 78 plots sampled in 2003 due to significant differences independent of grazing or other disturbance events (e.g., high rock cover or unusual bedrock type). We used 19 of the remaining 40 plots within BELA to balance our design with the correspondingly lower number of grazed plots. The subset of 19 plots was randomly sampled from the 40 plots, using geographic blocks as a stratification to spread our effort spatially. These 19 BELA plots, of the total 45 used in this study, have not been burned in the past 50 years and represent areas of unknown grazing status.

Only one plot was located at each site. Each macrolichen species encountered was assigned an abundance value: 1 = rare (<3 thalli), 2 = uncommon (4–10 thalli), 3 = common (<1% cover), 4 = abundant (1–5% cover), 5 = prolific (6–25% cover) and 6 = dominant (>26% cover). Lichen determinations were primarily based on Goward (1999), Goward et al. (1994) and Thomson (1984). We used thin-layer chromatography for identification of some *Bryoria*, *Cladonia*, *Hypogymnia* and *Stereocaulon*. All *Cladonia* identifications were based on voucher specimens with podetia, and strictly squamulose thalli were not recorded. Specimens from the *Cladonia phyllophora* and *C. cervicornis* groups were identified using Brodo and Ahti (1995). For ease in the field, we estimated cover of *Cladonia mitis* and *C. arbuscula*, isomorphs which require separation with spot tests using paraphenylenediamine, as a single lumped species and combined their cover values into a single variable (*Cladonia mitis/arbuscula*). UV light distinguished the two chemical species of *Thamnomia*, which were also collected from every site at which they occurred.

Vouchers are deposited at Oregon State University Herbarium (osc) and the National Park Service Herbarium in Anchorage, Alaska. A complete species list of the 78 BELA plots is available in Holt et al. (2007). Environmental measurements included slope, aspect, elevation, habitat factors (e.g., percent cover of rock, bare soil, open water and duff) and percent cover of general vegetation categories (e.g., shrub, subshrub, forb, graminoid, total bryophyte, total lichen and *Sphagnum*). Aspect and slope were transformed into estimates of potential annual direct incident radiation (McCune & Keon 2002).

Additional variables. Lichen mat condition and successional status were indicated using lichen height and successional scores. In other Arctic regions, land managers have used lichen height as a measure of site productivity (e.g., Ahti 1959; Steen 1965). This measure assumes that heavy grazing and other ground disturbances manifest as cropped or stunted lichens. Similarly, we assumed that taller lichens signified robust, undisturbed communities. In our study, heights of the same four lichen species (*Cladonia stygia*, *C. arbuscula/mitis*, *Cetraria cucullata* and *Cetraria laevigata*) were recorded, though not all four were necessarily present together at every plot. Strong linear relationships among heights from different species allowed us to average the four measurements, when available, into a single variable of average lichen height.

Finally, we created a variable to represent the successional status of each plot. In a previous study, we categorized 46 species into early, mid- or late successional stages using a synthesis of literature reports on succession following grazing and fire (Holt et al. 2006). Each species was assigned a successional species score of one, two or three to represent these early to late-successional stages, respectively. We used weighted averaging to combine our abundance estimates with these species scores yielding successional plot scores for each site.

Analyses. The coarse, approximately logarithmic, cover class scale alleviated the need to transform the community matrix. Most raw percent cover values for vegetation categories and substrate totals were not skewed, except for bare soil and total bryophyte cover. These were converted to proportions, and then arcsine-square root

transformed (Sokal & Rohlf 1995). Total bryophyte cover of one plot, 12L, fell far above the distribution of other plots, thus was deleted for all pair-wise comparisons of bryophyte cover.

We conducted univariate comparisons of lichen height, lichen species richness, successional scores, latitude, longitude, habitat factors and percent cover of general vegetation categories both between the two grazing levels as well as between geographic regions (i.e., north versus south and east versus west). Grazing and geographic multivariate comparisons were also conducted using lichen community composition. Most variables did not meet normality and constant variance requirements, discouraging the use of standard two-sample *t*-tests for comparisons. Therefore, we used multi-response permutation procedure (MRPP; Mielke 1984) for all comparisons in PC-ORD 5 (McCune & Mefford 2005). MRPP is a nonparametric permutation test that compares groups based on plot dissimilarity. Although normally a multivariate procedure, it can be applied to a single response variable as well. The effect size, or *A*-statistic, reflects the degree to which groups differ and is independent of sample size (McCune & Grace 2002). We used Sørensen distances to calculate community dissimilarity and Euclidean distances to assess dissimilarity among all other variables.

We also explored potentially confounding factors by investigating linear correlations between the univariate lichen characteristics (successional scores, total lichen cover, height and richness) and various aspects of the habitat and other vegetation. For these analyses, we combined the 19 BELA and 18 grazed plots. Of these correlations, we present only those $|r| \leq 0.50$. In addition, analysis of the eight fire plots was limited to observations of general trends. We avoided linear regressions of the fire plots due to our low sample size.

Nonmetric multidimensional scaling (NMS) depicted the multivariate relationships among plots (Kruskal 1964; Mather 1976). We ordinated plots of known grazing history with plots from BELA seeking compositional gradients associated with grazing that might aid in determining BELA's grazing history. The "slow and thorough" autopilot mode of PC-ORD sought the final configuration with the lowest stress and instability from multiple random starting

configurations. We used a maximum of 500 iterations in 250 runs of real data. The significance of the final configuration was tested as the proportion of randomizations with stress less than or equal to the observed stress, using 250 trials. Randomizations shuffled elements of the community matrix within species. The coefficient of determination is the variance represented in the relationship between Sørensen distance in the original matrix and the Euclidean distance in the ordination.

RESULTS AND DISCUSSION

Generalized recovery model. A small sample size and narrow range of years since burn limited our conclusions related to floristic recovery following fire. However, the general patterns in overall lichen and vascular plant cover do not appear to support our hypothetical recovery model (Fig. 1). Although lichen cover, as well as total bryophyte cover, varies with time since fire (Fig. 3A, B), vascular plant cover showed no trend with time since burn (Fig. 3C). This differential response suggests that the intensity or type of disturbance experienced by lichens and bryophytes in these eight plots may have been severe enough to induce a recovery sequence of immediate reduction in cover soon after the fire, followed by slow accumulation and subsequent decline with time. Meanwhile, these same disturbances had minor effects on vascular plant cover, which appears relatively unaltered by recent disturbance. While lichens and bryophytes have few perennating structures and are often destroyed by burning, many Arctic vascular plants are woody or suffrutescent and burnt stumps and buried rhizomes are usually capable of resprouting after light or moderate intensities of burning.

In sum, total vascular plant and lichen cover do not appear, at least directly, to interact in ways we predicted after fire. Lichen abundance increases from its initial low level and then decreases despite the steady level of vascular plant cover. Declines in lichen abundance with time, therefore, are likely not due to direct suppression or replacement by an accumulation of vascular plants over time as we expected. Instead, low lichen cover may be associated with other environmental factors or the disturbance itself.

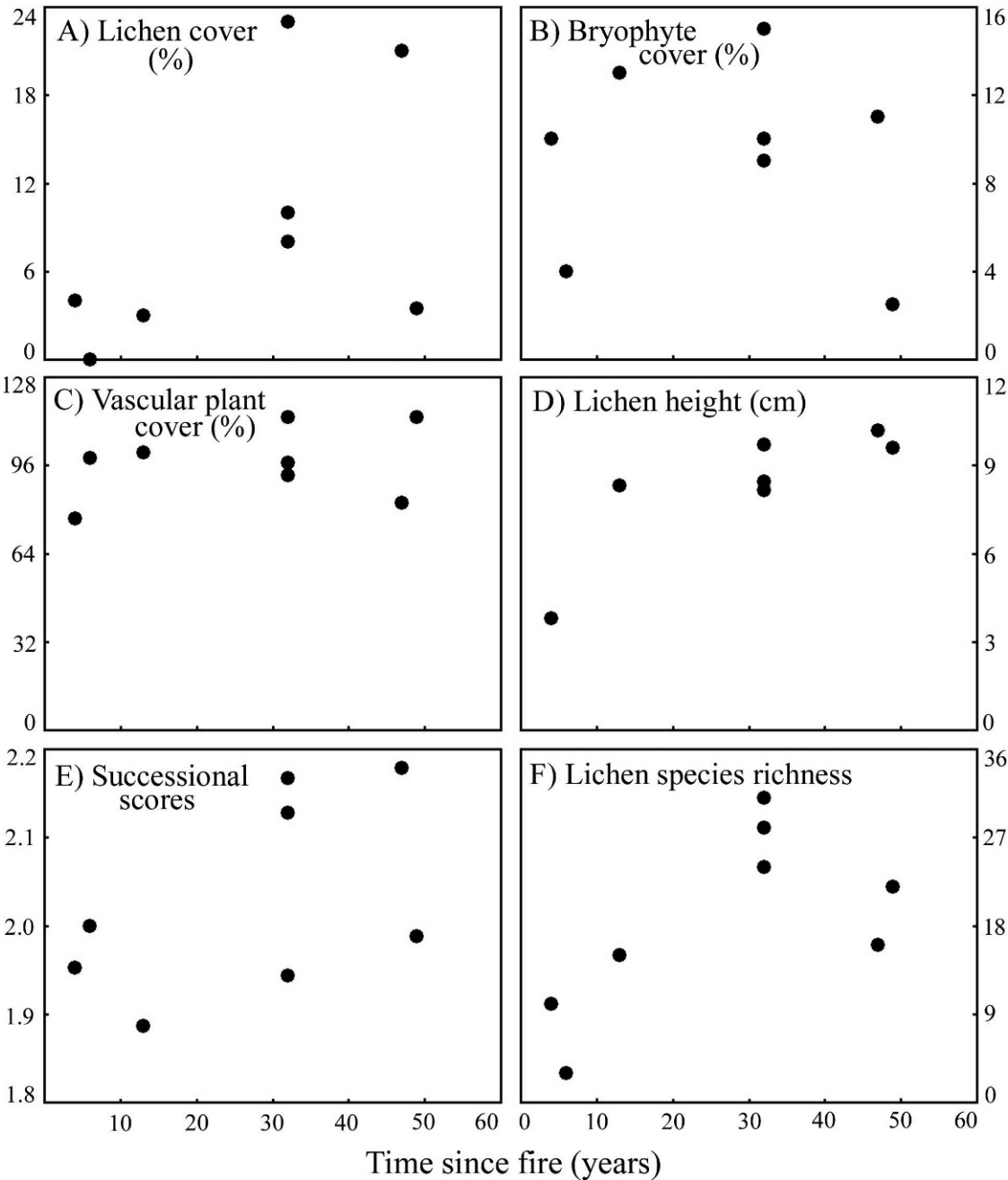


Figure 3. Scatterplots of time since fire (in years since burn) versus (A) total lichen cover (raw percent), (B) total bryophyte cover (raw percent), (C) total vascular cover (raw percent), (D) average lichen height in centimeters (reflected in seven points due to missing data at one site), (E) successional scores and (F) lichen species richness.

Average lichen height and successional scores increased with time since burn (Fig. 3D, E). This general increasing trend in successional scores, reflecting a progression from early to late-successional communities, was expected with greater

time since burn. Also, lichen height was used as a proxy for lichen biomass under the assumption that lichens were shorter with more recent or frequent disturbance, which was supported by our results. Several other studies have quantified lichen height

under this assumption (e.g., Ahti 1959; Steen 1965). Andreev (1954), however, suggested that over time, decomposition eventually exceeds growth and manifests as a decrease in lichen height. Such a decline was not evident in our 50-year chronosequence.

Lichen species richness also varied with time since burn (**Fig. 3F**). A subtle peak in richness may occur 30–40 years post-fire. Fire appears to directly reduce lichen species richness. In the two to three decades following fire, lichen species immigrate into the disturbed area, spreading from surrounding undisturbed patches, and accumulate over time. The decline in lichen species richness after 30 years may be due to a few lichen taxa, such as various species of *Cladina*, beginning to exclude others.

We found few comparable fire studies in the tundra (Racine 1981; Racine et al. 2004), yet studies from neighboring boreal forests report various patterns of lichen diversity and succession post-fire. Static lichen species diversity in various aged stands following fire has been reported for several boreal forests (Boudreault et al. 2000; Fortin et al. 1999). Fortin et al. (1999) further suggested that the same species found shortly after fire also occur in late-successional stages and only their spatial occupancy shifts in time. Conversely, a general trend of initial low diversity following disturbance, escalating to a peak and then a decline, as found in our lichen richness data, resembles many other findings in boreal regions (e.g., Coxson & Marsh 2001; Kershaw 1978). These studies proposed declines in lichen abundance and diversity due to late-successional canopy closure by spruce or pine, followed by lichen displacement by mosses. Reductions in lichen diversity accompany this displacement by both vascular plants and bryophytes (Boudreault et al. 2002; Morneau & Payette 1989).

Although these eight plots depict general patterns of recovery and floristic interactions, more data, especially from 1950s and older fires are needed to substantiate these trends. Moreover, our data suggest that post-fire recovery of lichens in dwarf shrub-graminoid dominated tundra requires more than 25 years, which was also proposed by Racine et al (2004). Furthermore, more data from long-term monitoring would benefit a comprehensive

understanding of lichen dynamics following tundra fires.

Grazing effects. Lightly grazed areas had, on average, taller lichens and greater total lichen cover than heavily grazed sites (**Tables 1, 2**). Lichen species richness, however, was roughly equal in heavily and lightly grazed sites. While no changes in richness were detected, minor yet statistically significant differences in community structure were observed between heavily and lightly grazed sites (**Table 1**). We also found that some lichen characteristics (total lichen cover and height) were related to various aspects of the habitat and other vegetation (**Fig 4**).

Geographic effects.—Potential effects of grazing might be confounded by geographic differences within the Seward Peninsula, perhaps mediated by climate or history. Average lichen height was greater in the western portions near Nome than on the eastern Seward Peninsula, and was higher still further north in BELA (**Table 2**). On the other hand, lichen cover and species richness did not significantly differ east to west within southern Seward Peninsula sites, yet both characteristics were substantially lower in BELA than all these southern plots combined. Minor yet statistically significant differences in lichen community structure occurred among all geographic comparisons (**Table 1**). Lastly, successional scores did not differ among all grazing and geographic comparisons (**Table 1**).

Lichen quantity.—Our results agree with other reports of lower lichen height associated with grazing (**Tables 1, 2**; e.g., Bergerud 1971; Helle & Aspi 1983; Kumpula 2001; Pegau 1970). We also found a moderate negative relationship of lichen height with bare ground cover ($r = -0.50$). The bare soil on the Seward Peninsula does not appear to result from grazing, because there was no difference in bare soil between grazing levels (MRPP near Nome; $A = -0.03$, $p = 0.50$). Rather, higher cover of bare ground indicates cryoturbation, local soil characteristics and a deficiency of plants able to survive in such conditions. Lichen architecture, quantified in our study as lichen height, reflects conditions associated with high bare soil, including lower competition and greater wind scour. On one hand, as surrounding vegetation of mosses and vascular plants increases, bare soil decreases. In such

Table 1. MRPP results from two comparisons based on geography and two based on grazing status. The *A*-statistic describes within-group homogeneity or the effect size of a difference. The probability that an observed difference in groups is due to chance is listed as *p*-values.

| | Geographic comparison | | Grazing comparison | |
|-------------------------------|----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|
| | North–South | East–West | Heavy–Light Nome | Heavy–Light South |
| SITE HISTORY | | | | |
| Location ¹ | BELA v. WestSP, EastSP | WestSP, EastSP | WestSP | WestSP, EastSP |
| Grazing Status | Unknown v. Light-Heavy | Light | Heavy v. Light | Heavy v. Light |
| Sample Size ² | 19 v. 18 | 7 v. 5 | 6 v. 5 | 6 v. 12 |
| GEOGRAPHY | | | | |
| Latitude | <i>A</i> = 0.57, <i>p</i> < 0.01 | <i>A</i> = 0.05, <i>p</i> = 0.21 | <i>A</i> = 0.04, <i>p</i> = 0.25 | <i>A</i> = 0.05, <i>p</i> = 0.16 |
| Longitude | <i>A</i> = 0.11, <i>p</i> < 0.01 | <i>A</i> = 0.71, <i>p</i> < 0.01 | <i>A</i> = 0.55, <i>p</i> < 0.01 | <i>A</i> = 0.22, <i>p</i> = 0.02 |
| LICHEN CHARACTERISTICS | | | | |
| Community Composition | <i>A</i> = 0.06, <i>p</i> < 0.01 | <i>A</i> = 0.03, <i>p</i> = 0.08 | <i>A</i> = 0.03, <i>p</i> = 0.05 | <i>A</i> = 0.02, <i>p</i> = 0.03 |
| Lichen Height | <i>A</i> = 0.21, <i>p</i> < 0.01 | <i>A</i> = 0.23, <i>p</i> = 0.03 | <i>A</i> = 0.62, <i>p</i> < 0.01 | <i>A</i> = 0.54, <i>p</i> < 0.01 |
| Lichen Cover | <i>A</i> = 0.11, <i>p</i> = 0.01 | <i>A</i> = 0.15, <i>p</i> = 0.06 | <i>A</i> = 0.51, <i>p</i> < 0.01 | <i>A</i> = 0.16, <i>p</i> = 0.02 |
| Lichen Richness | <i>A</i> = 0.31, <i>p</i> < 0.01 | <i>A</i> = 0.05, <i>p</i> = 0.22 | <i>A</i> = 0.05, <i>p</i> = 0.22 | <i>A</i> < 0.00, <i>p</i> = 0.39 |
| Successional Scores | <i>A</i> = 0.02, <i>p</i> = 0.14 | <i>A</i> = −0.01, <i>p</i> = 0.41 | <i>A</i> = 0.04, <i>p</i> = 0.27 | <i>A</i> = 0.10, <i>p</i> = 0.06 |
| OTHER VEGETATION | | | | |
| Total Vascular Plant Cover | <i>A</i> = 0.07, <i>p</i> = 0.02 | <i>A</i> = 0.27, <i>p</i> = 0.02 | <i>A</i> = −0.01, <i>p</i> = 0.40 | <i>A</i> = −0.01, <i>p</i> = 0.48 |
| Graminoid Cover | <i>A</i> = 0.11, <i>p</i> = 0.01 | <i>A</i> = 0.25, <i>p</i> = 0.02 | <i>A</i> = −0.05, <i>p</i> = 0.65 | <i>A</i> < 0.00, <i>p</i> = 0.36 |
| Total Bryophyte Cover | <i>A</i> = 0.04, <i>p</i> = 0.08 | <i>A</i> = 0.32, <i>p</i> = 0.02 | <i>A</i> = −0.05, <i>p</i> = 0.67 | <i>A</i> = −0.02, <i>p</i> = 0.53 |
| <i>Sphagnum</i> Cover | <i>A</i> = 0.35, <i>p</i> < 0.01 | <i>A</i> = 0.11, <i>p</i> = 0.10 | <i>A</i> = −0.03, <i>p</i> = 0.82 | <i>A</i> = 0.09, <i>p</i> = 0.07 |

¹ BELA = Bering Land Bridge National Preserve, WestSP = Western Seward Peninsula (Nome area), EastSP = Eastern Seward Peninsula.

² Prior to outlier deletions.

Table 2. Mean values of vegetation characteristics on the Seward Peninsula. Mean values in original units and standard deviation in parentheses. All values represent calculations prior to outlier deletions. Geographic comparisons include east to west (column A to B) and north to south (column D to E). Comparisons of grazing levels (light to heavy) were conducted strictly around the town of Nome in the western Seward Peninsula (column B to C) as well as throughout the southern Seward Peninsula, including both the eastern and western plots (column C to D).

| Column | A | B | C | D ¹ | E |
|-------------------------------|-------------------------|------------------|--------------------------|------------------------|-------------|
| Comparison | Grazing nome comparison | | | North-south comparison | |
| | East-west comparison | | Grazing south comparison | | |
| | Lightly Grazed | Lightly Grazed | Heavily Grazed | Lightly Grazed | Unknown |
| Grazing Status | Lightly Grazed | Lightly Grazed | Heavily Grazed | Lightly Grazed | Unknown |
| Location | Eastern Seward Pen. | West Seward Pen. | West Seward Pen. | WestSP, EastSP | BELA |
| Sample Size | 7 | 5 | 6 | 12 | 19 |
| LICHEN CHARACTERISTICS | | | | | |
| Height (cm) | 5.8 (0.5) | 7.7 (2.1) | 3.2 (0.8) | 6.6 (1.6) | 8.4 (1.8) |
| Lichen Cover (%) | 33.6 (21.2) | 54.0 (6.5) | 22.2 (11.5) | 42.1 (19.2) | 19.8 (12.2) |
| Richness | 31.0 (11.3) | 37.2 (4.9) | 32.8 (4.6) | 33.6 (9.4) | 21.4 (4.1) |
| Successional Scores (1–3) | 2.17 (0.11) | 2.23 (0.14) | 2.28 (0.05) | 2.19 (0.12) | 2.20 (0.07) |
| OTHER VEGETATION | | | | | |
| Vascular Plant Cover (%) | 79.0 (15.7) | 50.0 (18.5) | 62.8 (34.3) | 66.9 (22.0) | 87.5 (25.2) |
| Graminoid Cover (%) | 42.1 (18.0) | 13.4 (13.0) | 17.8 (18.3) | 30.2 (21.4) | 44.2 (15.5) |
| Bryophyte Cover (%) | 33.1 (15.5) | 7.4 (10.0) | 16.0 (21.2) | 22.4 (18.5) | 16.9 (17.2) |
| <i>Sphagnum</i> Cover (%) | 17.1 (18.5) | 2.4 (5.4) | 0.3 (0.8) | 11.0 (16.0) | 57.7 (34.8) |

¹ This column represents a combination of the first two columns (seven lightly grazed plots from the Seward Peninsula and 5 lightly grazed plots from Nome).

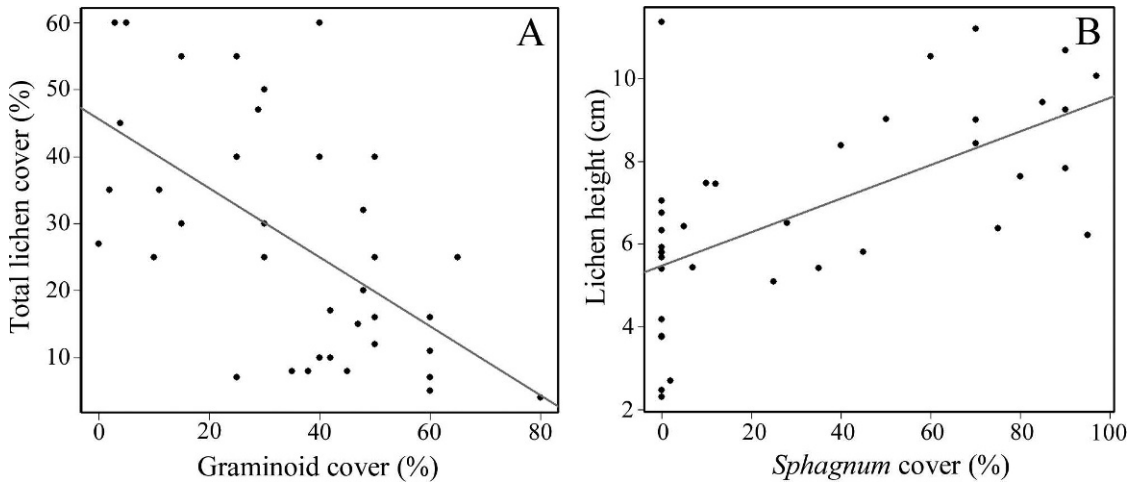


Figure 4. Scatterplots of (A) total lichen cover versus graminoid cover and (B) lichen height versus *Sphagnum* cover. Lichen cover and height, the only lichen characteristics that differed between grazing levels, were also strongly related to environmental factors. Graminoid and *Sphagnum* cover, respectively, were the strongest linear relationships to these variables. Black circles represent the 19 BELA plots and 18 grazed plots. The lines represent least-squares regression of these relationships.

environments, taller lichens more successfully compete for light. On the other hand, many sites high in bare soil tend to occur on more exposed, rocky ridge tops. Competition tends to be low in these extreme environments. Moreover, small, prostrate vegetation benefits from protection within the boundary layer, which minimizes evaporative losses and wind scour. Shorter lichens, therefore, are most likely to survive in these bare sites. Although lichen height varies with grazing level, some sites likely have shorter lichens due to site conditions.

Lichen height was also positively correlated with *Sphagnum* cover ($r = 0.66$; **Fig. 4B**). Over time, *Sphagnum* mats tend to increase in thickness, and lichens, competing for light, react by growing taller. Ahti (1959) further suggested that bog environments high in *Sphagnum* create microclimatic conditions that favor lichen growth. This apparent relationship between lichen height and *Sphagnum* cover, however, also appears unrelated to grazing. We found *Sphagnum* cover was consistent across lightly and heavily grazed sites (MRPP near Nome; $A = -0.03$, $p = 0.82$). In sum, the strongest linear relationships between lichen height and environmental factors, specifically cover of bare soil and *Sphagnum*, both appear independent of grazing. Regardless of these factors, comparison of lichen heights between levels of grazing show that grazing is clearly associated with reductions in lichen height.

Total lichen cover is also often reported to decline with grazing (e.g., Henry et al. 1995; Kumpula 2001; Staaland et al. 1993). Likewise, our results reveal lower total lichen cover in heavily grazed areas compared to lightly grazed or ungrazed sites (**Table 2**). Lichen cover also had a negative relationship with overall vascular plant cover and graminoid cover ($r = -0.54$ and -0.59 , respectively; **Fig. 4A**). Much research, substantiating the foundation for our recovery model following fire, suggests that lichens compete, albeit largely unsuccessfully, with vascular plants for space and sunlight (e.g., Coxson & Marsh 2001; Kershaw 1978). Prior research has proposed a positive relationship between caribou or reindeer and graminoids (Eskelinen & Oksanen 2006; Oksanen 1978; Post & Klein 1996). However, we found no such relationship as both total vascular plant and graminoid cover were similar in our heavily and lightly grazed plots (**Table 1**).

The negative relationship ($r = -0.54$) between cover of lichens and vascular plants in our grazing plots contrasts with patterns we identified in our fire plots. We acknowledge that fire and grazing disturbances greatly differ in type, intensity and duration, but suggest that patterns from one can help inform patterns of the other. Fluctuations in lichen abundance associated with recovery from fire are not directly correlated with vascular plant cover (**Fig. 3**).

Instead, we speculate that relationships between these two groups reflect indirect interactions of external factors determining distribution rather than direct interactions involving suppression or replacement. The strong negative relationship in our grazed plots may be more likely attributed to differing life strategies or environmental tolerances, enabling alternate groups to thrive in environments the other can barely survive and vice versa. Differences in lichen cover between the grazing levels, therefore, may be in response to the disturbance itself or factors of the local environment, yet not vascular plant abundance.

Despite some potentially confounding variables, we believe average lichen height is the best indication of grazing on the Seward Peninsula. Lichen height has a larger difference, as determined by the *A*-statistic, than lichen cover in discriminating grazed from ungrazed sites (**Table 1**). While lichen cover has been more frequently used as the primary indicator of grazing, few studies have also included lichen height as a surrogate measure (e.g., Ahti 1959; Steen 1965). In summary, we found lichen quantity, as measured in total cover and average height, was lower in heavily grazed sites compared to lightly or ungrazed sites.

Lichen quality.—Lichen species richness did not differ between levels of grazing on the Seward Peninsula (**Table 1**). Gilbert (1974) also reported that lichen species richness was unaffected by grazing. Conversely, grazing has been shown to both increase and decrease species diversity (Eskelinen & Oksanen 2006; Olofsson et al. 2001). Some investigators favor Connell's (1978) intermediate disturbance hypothesis to explain these disparities (Gaare 1995; Heggberget et al. 2002; Suominen & Olofsson 2000). They suggested that lichens depend on grazing by these animals to escape competition with vascular plants (Helle & Aspi 1983). Heavy grazing, however, may demolish entire lichen communities, and thus the greatest diversity is reached at moderate levels of grazing. Under this hypothesis, an idealized model of lichen richness as a function of grazing intensity might then be hump-shaped. We found a similar pattern mapping lichen species richness against time since fire (**Fig. 3F**). Fire and grazing differ in type, and can differ in intensity and frequency of

disturbance, yet the lichen community response may follow a similar pattern.

Lichen species richness increased with rock cover ($r = 0.52$). The presence of rocks diversifies substrates, which can manifest as increased species diversity. We also found negative correlations of lichen species richness with graminoid cover ($r = -0.58$), *Sphagnum* cover ($r = -0.57$) and latitude ($r = -0.62$). Latitudinal gradients in species diversity have been observed globally in many different organisms (Austrheim & Eriksson 2001; Scheiner & Rey-Benayas 1994). This relationship also accords with differences in richness between our north sites (averaging 21 species) and south sites (averaging 34 species). Environmental factors other than the level of grazing likely influence diversity.

Successional scores did not differ between grazing levels or between geographic areas (**Table 1**). These scores rely on reported shifts in lichen species composition stimulated by disturbances, such as grazing or fire. A lack of difference indicates that lichen species composition was nearly the same regardless of grazing history, that lichen species composition differed but both communities included species indicating the same successional stage, or that the successional scores do not accurately reflect the successional status of one or more areas. We first compared community structure between grazed and ungrazed areas to understand the lack of difference. If grazing produced a compositional shift, community structure would differ between grazed and ungrazed sites. We found minor differences in community structure between grazing levels (**Table 1**), which were too small to alter the successional scores despite differing grazing histories. Furthermore, the validity of these scores was supported by the expected increase in successional scores with time since disturbance in our fire plots (**Fig. 3E**). Therefore, major shifts in species composition associated with grazing may not occur on the Seward Peninsula, as they have been reported elsewhere, or perhaps grazing has been too sporadic or mild to induce such changes.

Although reductions in lichen quantity were associated with grazing, our results demonstrate that lichen quality, including lichen community structure and diversity, was unaffected or only minimally

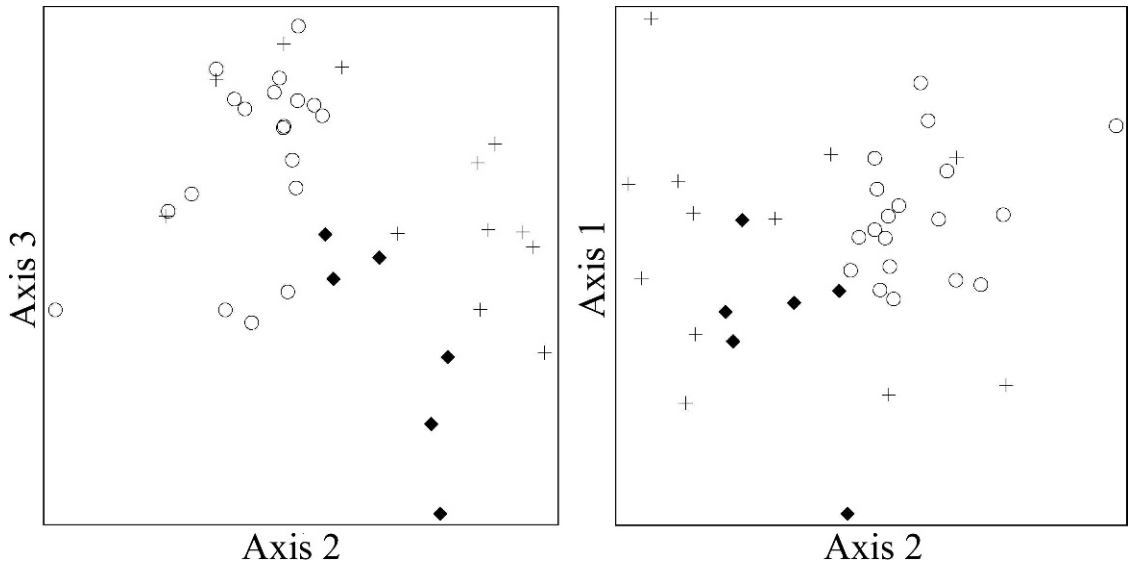


Figure 5. NMS 3-dimensional ordination of 19 BELA plots and 18 grazing plots in species space. BELA plots are shown in empty circles, heavily grazed sites as black triangles, and lightly grazed sites as pluses. BELA plots clearly cluster separate from most of the grazed plots, and do not appear to fit into a grazing gradient between the heavily and lightly grazed plots.

influenced by the levels of grazing experienced on the Seward Peninsula. Differences in lichen species richness were attributed not to grazing history but rather to latitude. Overall, grazing does not appear to have greatly altered lichen community composition or diversity on the Seward Peninsula, yet reductions in lichen height and cover appear to be associated with grazing.

Plots of unknown grazing history. The two primary lichen characteristics we found associated with grazing, lichen cover and height, were both significantly different between BELA plots, an area of unknown grazing history, and the grazed plots to the south (**Table 1**; **Fig. 2**). Taller lichens found within BELA might initially suggest less grazing in the Preserve as compared to the remainder of the Seward Peninsula; however, plots within BELA also had more *Sphagnum* cover (**Table 2**). As stated earlier, lichen height may increase in environments high in *Sphagnum*, independent of grazing (**Fig. 4B**). We also found that plots within BELA had lower lichen cover than sites to the south (**Table 2**). From a grazing perspective, reductions in cover may be associated with more frequent, intense or recent use. Yet plots from BELA were also higher in overall vascular plant and graminoid cover (**Tables 1, 2**), indicating site or climatic differences which may manifest as lower

lichen cover. Finally, BELA plots were lower in average lichen richness than plots in the southern Seward Peninsula (**Tables 1, 2**). We do not assume this reduction reflects severe over- or undergrazing, as proposed by the intermediate disturbance hypothesis. Trends of decreasing diversity with higher latitude observed elsewhere may provide a better explanation (e.g., Austrheim & Eriksson 2001; Scheiner & Rey-Benayas 1994). BELA is in the far northern portion of the peninsula, which is consistent with our findings of lichen species richness decreasing with latitude.

Ordination of grazing and BELA plots combined yielded a three-axis solution in NMS that was stronger than expected by chance, based on a randomization test ($p = 0.004$). The best solution yielded a final stress value of 15.3. The final instability was 0.0002 and there were 500 iterations in the final solution. Cumulatively, these three axes represented 81.6% of the community variation (**Fig. 5**). Plots from BELA did not nest between the heavily and lightly grazed plots, as may be expected if there were a grazing continuum with BELA somewhere in the middle. Instead, BELA plots clearly separated away from the grazed plots, which in themselves did not appear to form a clear grazing gradient (**Fig. 5**). Separation of BELA plots from the

Table 3. Lichen species occurring in more than 50% of the 12 lightly grazed plots. “Freq” is the number of the lightly grazed plots in which the species occurred. The remaining columns indicate the distribution of abundance estimates (rare = <3 thalli, uncommon = 4–10 thalli, common = <1% cover, abundant = 1–5% cover, prolific = 6–25% cover and dominant = >26% cover) within each of the plots in which it occurs.

| Species | Freq | Rare | Uncommon | Common | Abundant | Prolific | Dominant |
|---|------|------|----------|--------|----------|----------|----------|
| <i>Alectoria nigricans</i> (Ach.) Nyl. | 9 | 6 | 2 | 1 | 0 | 0 | 0 |
| <i>Alectoria ochroleuca</i> (Hoffm.) A. Massal. | 6 | 1 | 3 | 2 | 0 | 0 | 0 |
| <i>Asahinea chrysantha</i> (Tuck.) W. L. Culb. & C. F. Culb. | 6 | 1 | 1 | 3 | 1 | 0 | 0 |
| <i>Bryocaulon divergens</i> (Ach.) Kärnefelt | 7 | 1 | 3 | 2 | 1 | 0 | 0 |
| <i>Cetraria cucullata</i> (Bellardi) Ach. | 12 | 0 | 4 | 6 | 2 | 0 | 0 |
| <i>Cetraria islandica</i> (L.) Ach. | 6 | 2 | 3 | 0 | 1 | 0 | 0 |
| <i>Cetraria kamczatica</i> Savicz | 6 | 0 | 2 | 3 | 1 | 0 | 0 |
| <i>Cetraria laevigata</i> Rass. | 12 | 1 | 2 | 6 | 3 | 0 | 0 |
| <i>Cetraria nivalis</i> (L.) Ach. | 10 | 3 | 2 | 4 | 1 | 0 | 0 |
| <i>Cladonia amaurocraea</i> (Flörke) Schaer. | 11 | 1 | 5 | 3 | 2 | 0 | 0 |
| <i>Cladonia bellidiflora</i> (Ach.) Schaer. | 7 | 5 | 2 | 0 | 0 | 0 | 0 |
| <i>Cladonia coccifera</i> (L.) Willd. | 8 | 6 | 1 | 1 | 0 | 0 | 0 |
| <i>Cladonia maxima</i> (Asahina) Ahti | 8 | 1 | 3 | 3 | 1 | 0 | 0 |
| <i>Cladonia subfurcata</i> (Nyl.) Arnold | 8 | 3 | 4 | 1 | 0 | 0 | 0 |
| <i>Cladonia sulphurina</i> (Michx.) Fr. | 6 | 2 | 4 | 0 | 0 | 0 | 0 |
| <i>Cladonia uncialis</i> (L.) F. H. Wigg. | 12 | 3 | 2 | 4 | 2 | 1 | 0 |
| <i>Cladina arbuscula</i> (Wallr.) Hale & W. L. Culb./ <i>C. mitis</i> (Sandst.) Hustich | 12 | 0 | 0 | 4 | 6 | 2 | 0 |
| <i>Cladina rangiferina</i> (L.) Nyl. | 10 | 0 | 4 | 5 | 0 | 1 | 0 |
| <i>Cladina stellaris</i> (Opiz) Brodo | 9 | 3 | 0 | 2 | 4 | 0 | 0 |
| <i>Cladina stygia</i> (Fr.) Ahti | 12 | 0 | 1 | 4 | 3 | 4 | 0 |
| <i>Lobaria linita</i> (Ach.) Rabenh. | 6 | 2 | 2 | 1 | 1 | 0 | 0 |
| <i>Nephroma arcticum</i> (L.) Torss. | 9 | 3 | 3 | 3 | 0 | 0 | 0 |
| <i>Parmelia omphalodes</i> (L.) Ach. | 6 | 1 | 3 | 2 | 0 | 0 | 0 |
| <i>Sphaerophorus globosus</i> (Huds.) Vain. | 9 | 1 | 2 | 5 | 0 | 1 | 0 |
| <i>Stereocaulon paschale</i> (L.) Hoffm. | 7 | 0 | 1 | 3 | 3 | 0 | 0 |
| <i>Thamnolia subuliformis</i> (Ehrh.) Culb. | 7 | 2 | 3 | 2 | 0 | 0 | 0 |
| <i>Thamnolia vermicularis</i> (Sw.) Ach. ex Schaer. | 6 | 1 | 4 | 1 | 0 | 0 | 0 |

grazed plots to the south may reflect differences in locality rather than grazing that manifest as divergent lichen community composition.

Since we know few details of the grazing history in BELA, we cannot attribute disparities in lichen characteristics between BELA and southern Seward Peninsula plots to grazing. Our results suggest that BELA is located in an environment more favorable to vascular plants and *Sphagnum*, and lichens grow taller in response. Furthermore, lichen communities in BELA are less prolific and diverse than their southern counterparts, but perhaps primarily because of their locality or associated climatic differences. Such climatic influences are evident in other Arctic tundra and heath systems where global

warming induces declines in lichen biomass and abundance as a function of increased abundance of vascular plants (Cornelissen et al. 2001).

We present a list of the most common lichen taxa, or those occurring in greater than 50% of the lightly grazed plots (Table 3). The frequency and abundance of these species may serve as a reference or baseline for future comparisons. In conclusion, the Seward Peninsula, including BELA, currently supports diverse and abundant lichen communities. Given rebounding caribou populations, potential interest in revitalizing the reindeer industry and the rapid pace of global warming, it is critical to monitor an interaction between climate change and grazing. In the future, experimental studies and long-term

monitoring are necessary to substantiate patterns and possible changes of the lichen communities on the Seward Peninsula.

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